

Research Article

Three new species of plexippine jumping spiders (Salticidae, Salticinae, Plexippini) from dry forest in Boeny region, north-western Madagascar

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Abstract

Despite being the most diverse family of spiders, Salticidae (jumping spiders) are poorly studied in Madagascar with only 47 of the total 105 species recorded in the last 100 years. Here, we describe three new species of Plexippini Simon, 1901 from dry forests in North-western Madagascar as part of an ongoing biomonitoring programme. This paper increases the number of species in the genus *Evarcha* Simon, 1902 from 93 to 95 and *Thyene* Simon, 1885 from 55 to 56. Additionally, we publish specimen records of *Plexippus petersi* (Karsch, 1878) from Madagascar for the first time. All new species are diagnosed and illustrated through photographs and drawings.

Key words: Afrotropics, discovery, *Evarcha*, new record, new species, taxonomy, *Thyene*



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Introduction

Salticidae (Araneae) is the most diverse family of spiders in the world, with 6,654 species known from 681 genera (WSC 2024). More than 1,000 salticid species are known from the Afrotropical region; however, sampling remains geographically biased and not of equal coverage. The salticid fauna of many areas is still poorly studied and understood. Madagascar has 105 species of salticid recorded from 40 genera (WSC 2024). Yet, of the 105 species, only 47 have been documented in the past 100 years (WSC 2024). Madagascar has long been recognised as a global biodiversity hotspot (Mittermeier et al. 1998, Myers et al. 2000) where habitat diversity and endemism, proportionate to land area, are especially pronounced in a global sense (Mittermeier et al. 2011). The limited research on spiders on Madagascar to date highlights the high numbers of undescribed species (Wood 2008; Jäger 2020; Griswold et al. 2022).

The Plexippini of Madagascar include several genera whose boundaries are unclear. Species of *Evarcha* Simon, 1902 are generally separated from their closest morphologically resembling relative in *Hyllus* C. L. Koch, 1846 by a narrower carapace not clearly wider than eye field (vs. much

more rounded, clearly wider than eye field), and with epigynal pockets (vs. absent). *Evarcha madagascariensis* Prószyński, 1992 is the sole representative of its genus on the island, known from a single holotype male. *Thyene* Simon, 1885 are flattened plexippines with a strong stout leg I, tufts of distinct dark bristles lateral to posterior of ALEs and relatively homogenous pedipalps, with a circular tegulum twice encircled by the embolus and a thin tibial apophysis (Wesołowska 2006). Three species of *Thyene* are known from Madagascar, with none recorded through positive specimen identification since 1908.

A biodiversity inventory focusing on an area of enigmatic dry forests in Mariarano, north-western Madagascar has been collecting spiders as part of a biomonitoring project in 2017, 2018 and 2023 by the Biodiversity Inventory for Conservation (BINCO; www.binco.eu), Operation Wallacea (www.opwall.com), and the Development and Biodiversity Conservation Action for Madagascar (DBCAM). Previous work in the area (Fig. 1) has discovered numerous putative endemics, e.g. a couple of new spider species to date (Jocque et al. 2017; Jocqué and Jocque 2021; Pett and Rabemananjara 2022), with many more in preparation. We begin the process of tackling the salticids of the area with this project on the Plexippini Simon, 1901 fauna. The aims and objectives of this study are to describe three new species and report the first specimen record of *Plexippus petersi* (Karsch, 1878) from Madagascar.

Materials and methods

Spiders were collected in June–August 2017, 2018, 2023 during an expedition in north-western Madagascar. All material is preserved in 70% ethanol. The left pedipalp of several males were dissected and illustrated. The illustrated female epigynes were first dissected using a custom-made fine hooked needle to excise the epigynal plate, digested in warm lactic acid solution for 3–5 minutes before being observed in methyl salicylate. The cleared epigyne was temporarily prepared on a slide and examined with a compound microscope. Examinations were carried out with an AmScope ZM-4T stereomicroscope or an Olympus BX61. Images were taken using either a Zeiss Discovery V12 with an Axiocam 208 colour camera. All images were z-stacked with between 10–30 images merged into a single photomontage using Helicon Focus 6.7 (www.helicon-soft.com). Images were adjusted in Adobe Photoshop version 21.0.1 for contrast and white balance. Drawings of genitalia were made by KM. Plates were also composed in Adobe Photoshop. All measurements are in millimetres (mm). Maps were made with simplemappr (Shorthouse 2010).

Abbreviations: **AER** = anterior eye row, **AL** = abdomen length, **AME** = anterior median eyes, **ALE** = anterior lateral eyes, **AW** = abdomen width, **CD** = copulatory ducts, **CH** = carapace height, **CL** = carapace length, **CW** = carapace width, **PME** = posterior median eyes, **PLE** = posterior lateral eyes, **PER** = posterior eye row, **SL** = sternum length, **ST I & ST II** = spermathecae I (posterior) and II (anterior), **SW** = sternum width, **TL** = total length, **ORW** = ocular row width.

Collection abbreviation: **RMCA**—Royal Museum for Central Africa, Tervuren, Belgium (A. Henrard & D. Van den Spiegel).



Figure 1. Type locality of all three new species.

Results

Taxonomy

Family Salticidae Blackwall, 1841

Subfamily Salticinae Blackwall, 1841

Clade Salticoida Maddison & Hedin, 2003

Tribe Plexippini Simon, 1901

Subtribe Plexippina Maddison, 2015

Genus *Evarcha* Simon, 1902

Type species. *Evarcha falcata* (Clerck, 1757), by subsequent designation.

Diagnosis. *Evarcha* are medium-sized plexippine salticids displaying a vast diversity in genital morphology: the embolus may be short, stout and compact or range to very long and filamentous; tegulum ranges from round, oval to conical and may bear distinctive outgrowths/ expansions; single RTA present; insemination ducts range from broad and membranous to thin and tube-shaped; Leg III longer than IV (Wang et al. 2024; Zamani et al. 2017; Žabka 1993). However, it has been suggested that *Evarcha*, as currently defined, acts as a ‘dumping ground’ genus and likely harbours many unrelated species, and cryptic generic diversity (Kanesharatnam and Benjamin 2020). Thus, a universal definition of the genus is difficult to propose (Wang et al. 2024).

***Evarcha tsipikafotsy* sp. nov.**

<https://zoobank.org/55A72979-FAFC-4D36-86D2-83E4BEA4B77D>

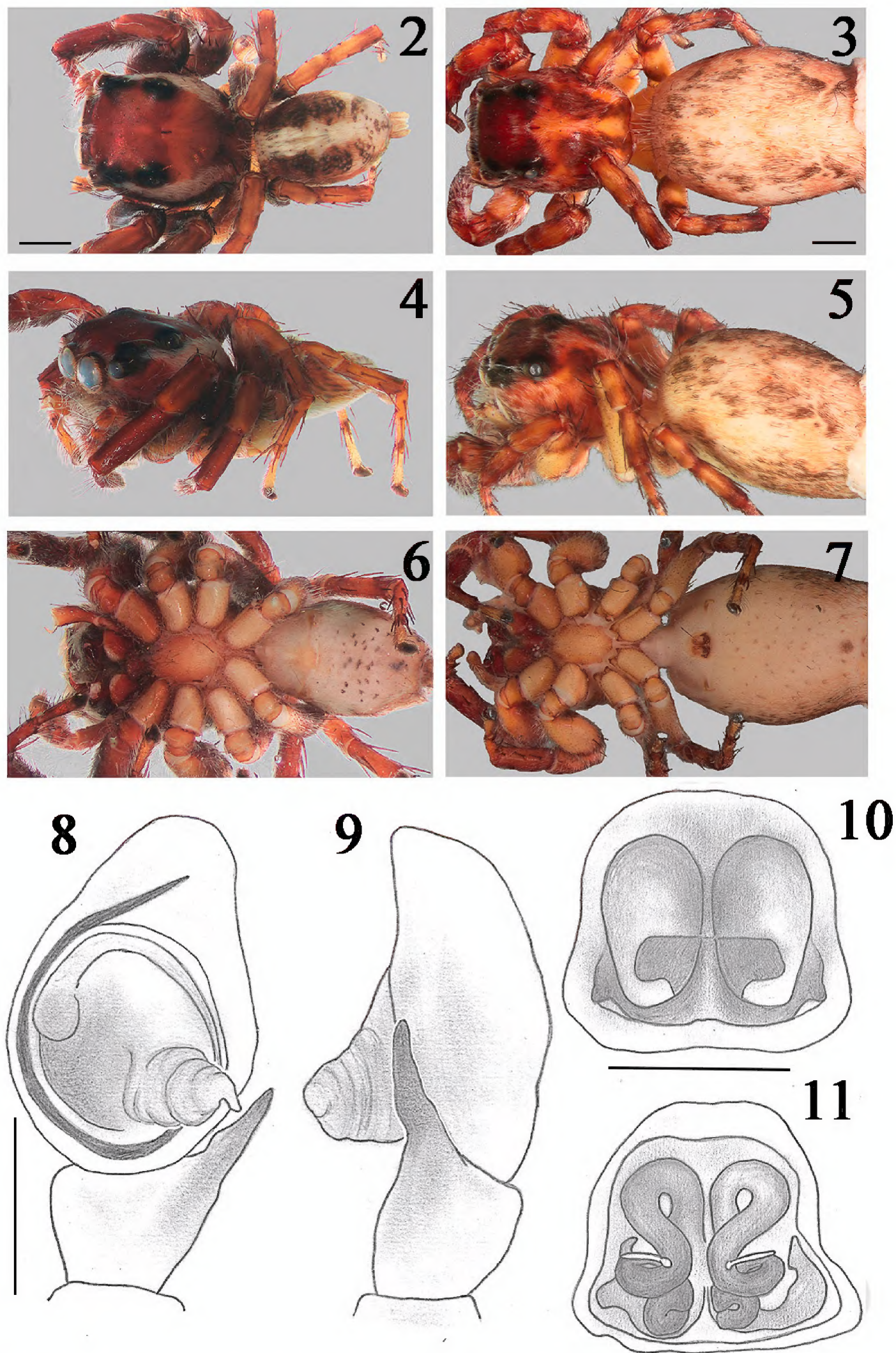
Figs 2–19

Material examined. Holotype • ♂: MADAGASCAR; Mahajanaga province, Mariarano classified forest, Antafiameva camp; 15.46°S, 46.74°E; 12 July 2017, 20:06; “Savannah next to dry forest”, Jonas Merckx leg. (BE_RMCA_ARA.Ara.247698).

Paratypes • 1 ♀ MADAGASCAR; Mahajanaga province (all), Mariarano classified forest (all), Mariarano camp; 15.48°S, 46.69°E; 17 June 2018, 20:06; “Savannah next to dry forest”, Jonas Merckx leg. (BE_RMCA_ARA.Ara.247699) Mariarano camp, • 1 ♂; 15.29°S, 46.41°E; 20 June 2023, 09:00; “Margin of tropical dry forest”, Jaime Escobar-Toledo leg. (BE_RMCA_ARA.Ara.247700) Mariarano camp, • 1 ♀; 15.29°S, 46.41°E; 22 June 2023, 20:30; “Margin of tropical dry forest”, Jaime Escobar-Toledo leg. (BE_RMCA_ARA.Ara.247701) Mariarano camp, • 1 ♀; 15.29°S, 46.41°E; 23 June 2023, 8:30; “Margin of tropical dry forest”, Jaime Escobar-Toledo leg. (BE_RMCA_ARA.Ara.247702) Matsedroy camp, • 1 ♂; 15.29°S, 46.39°E; 3 July 2023, 10:00; “Open tropical dry forest”, Jaime Escobar-Toledo leg. (BE_RMCA_ARA.Ara.247703) Matsedroy camp, • 1 ♂; 15.29°S, 46.39°E; 9 July 2023, 21:00; “Open tropical dry forest”, Jaime Escobar-Toledo leg. (BE_RMCA_ARA.Ara.247704) Matsedroy camp, • 1 ♂, 1 ♀; 15.29°S, 46.38°E; 11 July 2023, 19:45; “Tropical dry forest”, Jaime Escobar-Toledo leg. (BE_RMCA_ARA.Ara.247705) Mariarano camp, • 1 ♂; 15.29°S, 46.41°E; 16 July 2023, 08:00; “Margin of tropical dry forest”, Jaime Escobar-Toledo leg. (BE_RMCA_ARA.Ara.247706).

Etymology. The specific epithet is a noun in apposition, amalgamating the Malagasy words for “stripes” (tsipika) and “White” (fotsy) (this is the correct conjugation of the words in Malagasy). Reference is made to the stripes of white setae on the lateral parts of the carapace.

Diagnosis. *Evarcha tsipikafotsy* sp. nov. is distinctive in palpal conformation from most *Evarcha*, with a similar body form and colour pattern. *Evarcha tsipikafotsy* is most similar in palpal conformation to *E. madagascariensis* Prószyński, 1992 (Madagascar) and *E. patagiata* (O. Pickard-Cambridge, 1872) (The Levant) in sharing a singular large RTA, an embolus running clockwise along edge of cymbium for over 1/3 cymbium length and a moderate posterior tegular expansion. *Evarcha tsipikafotsy* sp. nov. is clearly separated from those species by (i) posterior tegular expansion that is projected distinctly at 4 o’clock position with a separate finger-like protrusion (vs. projected at 5 o’clock position without finger-like protrusion or small projection at 6 o’clock position, respectively); (ii) embolus that is about 2/3 length of cymbium and follows margin (vs. just under 1/2 length of cymbium in both species, additionally embolus is projected a small distance away from tegulum in *E. patagiata*); (iii) RTA that is sinuous at apex (vs. not with sinuous apex); additionally, *Evarcha tsipikafotsy* sp. nov. is further separated from *E. madagascariensis* by having only a small RL cymbial expansion (vs. very large), and an RTA that does not make contact with RL cymbial expansion (vs. does make contact). Females are most similar in epigynum conformation to *E. arcuata* (Clerck, 1757) (Most of Europe, Northern Asia, Libya and Mexico) with coiled CD and moderately large epigynal atria (separated by a distinctive arch). *Evarcha tsipikafotsy* sp. nov. is clearly separated from *E. arcuata* by: (i) thick tightly coiled CD (vs. thin, less tightly coiled); (ii) FD approximately halfway up the epigynal region (vs. 3/4 vertically high),



Figures 2–11. *Evarcha tsipikafotsy* sp. nov. **2, 4, 6** male holotype habitus **3, 5, 7** female paratype habitus **8, 9** male pedipalp **10, 11** female epigyne **2, 3, 11** dorsal **4, 5** lateral **3, 6, 7, 8, 10** ventral **9** retrolateral. Scale bars: 1 mm (**2–7**); 0.5 mm (**8–11**).

(iii) epigynal arch long and thin (vs. short and broader), (iv) atria large and deep, about $\frac{3}{4}$ entire surface of epigynal region (vs. much smaller, about $\frac{1}{4}$ surface of epigynal region).

Taxonomic notes. *Carrhotus harringtoni* Prószyński, 1992 external epigyne resembles *E. tsipikafotsy* sp. nov., but the internal ST and CD are markedly different from species of *Evarcha* s. s., with large oval ST and a simpler CD pattern that is closer to *Carrhotus* species than to that of *Evarcha*. However, we consider the generic identity of *C. harringtoni* to be unclear and require further investigation.



Figures 12, 13. *Evarcha tsipikafotsy* sp. nov. in vivo images, male. Photo credits: J.E.T.

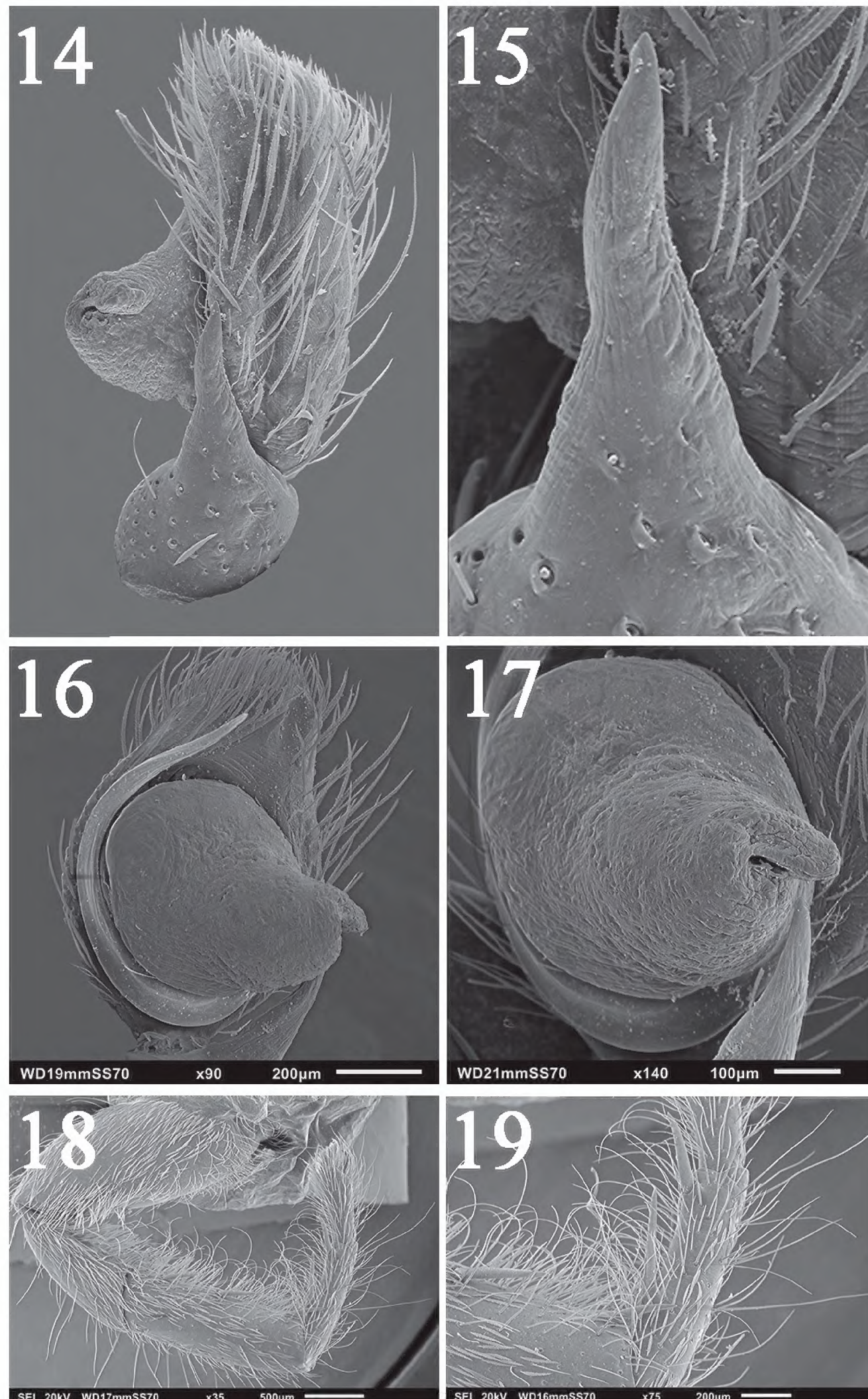
Description. Male (holotype). Measurements. TL 6.48, CL 3.48, CW 2.96, CH 2.2, SL 1.36, SW 0.92, AL 4, AW 2.04, chelicera length 1.2, chelicera width 0.64. Legs. I: 2.56, 1.88, 1.8, 1.16, 0.96. II: 2, 1.24, 1.36, (remaining segments missing). III: 2.84, 1, 1.28, 1.08, 0.92. IV: 2.36, 1.04, 1.4, 1.04, 0.56. Eyes: AME – 0.62, ALE – 0.32, PME – 0.1, PLE – 0.26, ORW – 0.236.

Colouration: Carapace generally orangish-brown, dark brown in vivo, with lateral fringes of white setae just ventral to PER, band of sparser black setae ventral; chelicerae brown; legs 1,2 brownish; legs 3,4 orangish; coxae pale beige both dorsally and ventrally; abdomen generally beige with a mostly contiguous white band down abdomen centre, venter beige with sparse brown spots (figs 12, 13).

Carapace: High, flat, declining sharply just posterior to fovea, foveal depression very shallow; several very long setae projected anteriorly just ventral of PME; fringe of white setae mid-length and appressed to carapace; sparse patches of white setae between eyes. **Sternum:** Oval shape, widest around midpoint. **Legs:** Legs 1,2 slightly broader; dense fringe of setae on patellae & tibiae I & II. **Chelicerae:** One tooth on retromargin, two teeth on promargin, retromarginal tooth larger than largest promarginal tooth, promarginal teeth close together with apical one three times the size of smallest one. **Abdomen:** Ovoid, widest halfway along length; several longish thick white setae protrude at a 45°–30° angle at anterior margin; venter dull. **Leg spination:** I: F 3d 2pl, P 1d 2pl 2rl, Ti 2pl v3-3, Mt v2-2. II: F 3d 1pl 2rl, P 1pl 1rl, Ti 3pl 3v, Mt v2-2. **Pedipalp:** Cymbium orange to brown; RTA thick, comparable length to the tibia, protrudes along edge of cymbium without another point of contact; tegulum circular with sperm duct dark red to brown, follows curve of tegulum clockwise from 9 o'clock to behind the tegular expansion at 5 o'clock; long embolus originating from 5 o'clock behind tegular expansion in ventral view and contours the edge of the tegulum before branching off at 10 o'clock and up towards apex of the cymbium (figs 14–19).

Female. Measurements. CL 4.12, CW 3.28, CH 2.42, AL 7.08, AW 4.20, SL 1.72, SW 0.86, Leg measurements: I: 2.24, 1.32, 1.72, 1.20, 0.68. II: 1.92, 1.20, 1.42, 1.00, 0.76. III: 2.80, 1.32, 1.50, 1.72, 0.88. IV: 2.56, 1.08, 1.72, 1.76, 0.84. Eyes: AME 0.64, ALE 0.38, PME 0.12, PLE 0.32.

Leg spination: I: F 4d 2pl, P 1d, Ti v3-3, Mt v2-2. II: F 3d 2pl, P 1d, Ti pl2 v3-3, Mt v2-2.



Figures 14–19. *Evarcha tsipikafotsy* sp. nov. S.E.M micrographs 14–17 male left pedipalp 18, 19 leg I 14, 15- retrolateral 16, 17- ventral to prolateral 18 prolateral dorsal 19 prolateral dorsal detail of tibia.

General colouration, pattern and somatic morphology the same as in male. Except; carapace slightly lighter and mottled, dark brown-black patches around eyes from ORW to fovea, much sparser fringe of white setae and no band of black setae on carapace, no vertical stripes on abdomen, instead beige with interspersed patches of beige, brown and black setae.

Epigyne: epigynal region longer than wide by about 1.5×; copulatory openings at anterior margin directed anteriorly, CD long and thin, directed straight posteriorly, suboval ST moderately large, separated by about half their width.

***Evarcha vavannyangisy* sp. nov.**

<https://zoobank.org/3A76F40D-4E6C-4E93-88D3-E2A065188704>

Figs 20–25

Material examined. Holotype • ♂: MADAGASCAR; Mahajanaga province, Mariara-no classified forest, Matsedroy camp; 15.471°S, 46.744°E; 13 July 2017, 20:06; “Savannah next to dry forest”, Yi Wang leg. (BE_RMCA_ARA.Ara.247707).

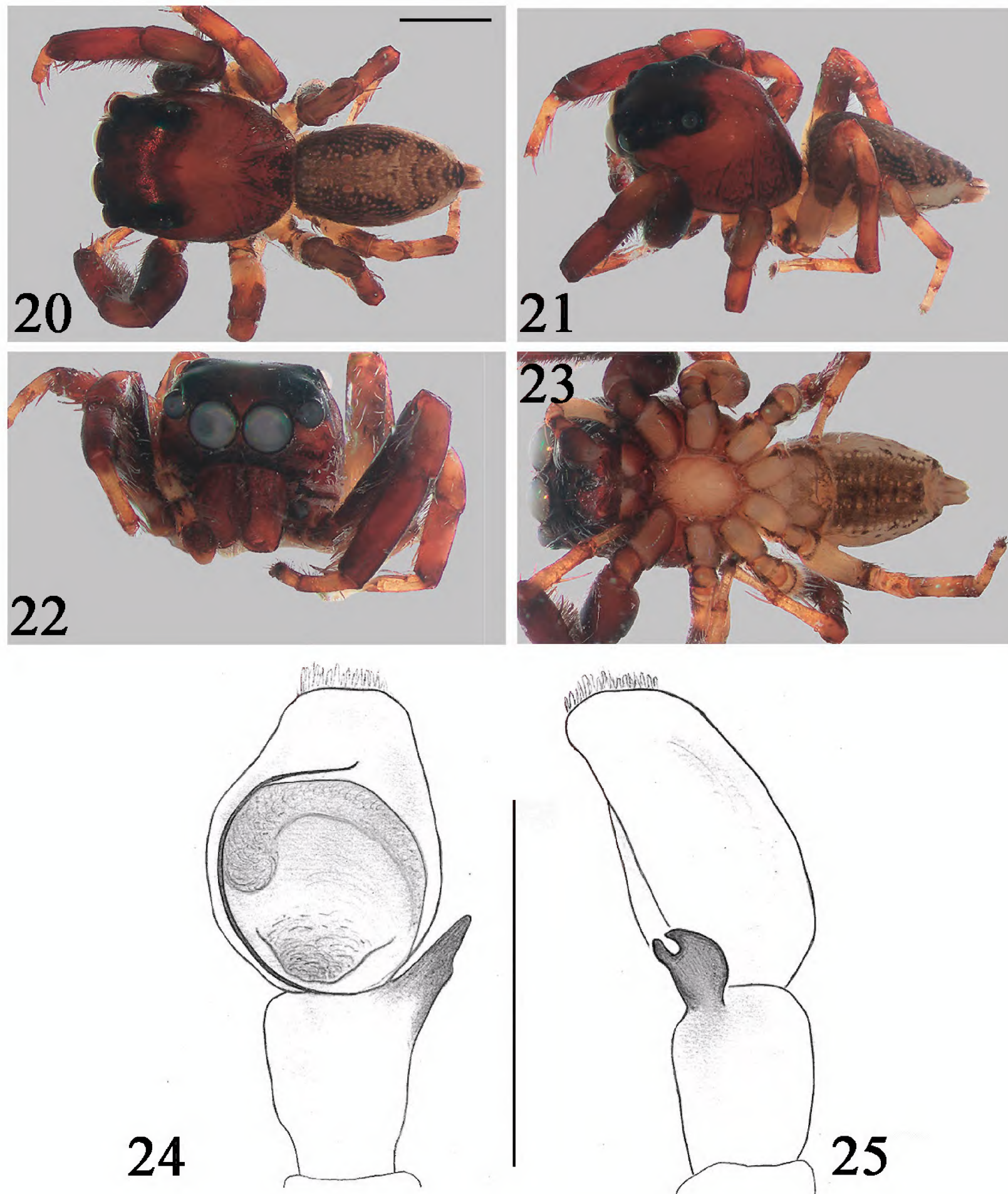
Etymology. The specific epithet is a noun in apposition, amalgamating the Malagasy words for “squid” and “beak”. Reference is made to the bifurcated RTA.

Diagnosis. *Evarcha vavannyangisy* sp. nov. is highly distinctive in the genus. However, some similarities in palpal conformation exist with *E. zayu* Wang, Mi & Li, 2024 (China) and *E. amanzi* Wesolowska & Haddad, 2018 (South Africa). *E. vavannyangisy* shares a bifurcated RTA, basomedian tegular expansion and embolus approximately half the perimeter of the bulb with *E. zayu*, but can be separated by: (i) deeply bifurcated RTA (vs. shallow); (ii) very small basomedian tegular bump (vs. very pronounced tegular expansion); and (iii) embolus slender for its entire length (vs. much broader). Additionally, *E. zayu* is from mainland China. *E. vavannyangisy* sp. nov. shares a deeply bifurcated RTA with only one congener, *E. amanzi* Wesolowska & Haddad, 2018 (South Africa), but can be readily separated by: (i) basomedian tegular expansion very small (vs. well projected posteriorly); and (ii) embolus runs approximately half the perimeter of the bulb (vs. arising 10 o'clock position and running until 12 o'clock position).

Description. Male (holotype). Measurements. CL 2.68, CW 2.36, AL 2.44, AW 1.56, SL 1.00, SW 0.76. Leg measurements: I: 1.80, 0.88, 1.64, 1.04, 0.56. II: 1.40, 0.76, 0.84, 0.68, 0.44. III: 2.04, 0.84, 1.20, 1.00, 0.60. IV: 1.32, 0.60, 0.84, 0.90, 0.56. PME 0.11, PLE 0.20, ALE 0.30, AME 0.56.

Colouration: Carapace generally brownish orange, black patches around eyes, white setae ventral to PLE, scant black mottling at posterior margin. Chelicerae, maxilla, labium, deep reddish brown. Sternum & coxae pale brownish. Leg I dark reddish brown, legs II – IV generally brownish, with pale basal half of femorae. Abdomen generally brownish, with considerable alternations between pale and black mottlings, venter cream with black mottling. **Carapace:** generally rounded, very slightly longer than wide, moderately high, highest at PLE. Long, sparse, fine white setae around clypeus directed medially. **Sternum:** suboval, about 1.5× long as wide. **Legs:** Leg I much broader, with field of long, erect setae ventrally on Ti I. Field of long white prolateral ventral setae on patellae I. **Abdomen:** oval, about twice as long as wide. **Pedipalp:** femur slightly longer than patella and tibia together; many long fine setae prolaterally on tibia, long setae thicker retrolaterally, RTA about 0.8× length of tibia, projected at 1 o'clock position, bifurcated with squid-beak-like appearance, rounded ventral element and sharp pointed dorsal element; cymbium almost as long as tibia, with truncated anterior margin, tegulum round, embolus slender, wrapping around tegulum for just over half a turn, arising at 5'30 position and terminating at around 0'15 position, very small basomedian tegular bump.

Leg spination: I: F d2 pl, P pld1, Ti pl2 v3-3, Mt v2-2. II: F pl2 d2 rl2, P pl1 d1, Ti pl2 v3-3, Mt v2-2.



Figures 20–25. *Evarcha vavannyangisy* sp. nov. 20–23 male holotype habitus 24, 25 male pedipalp 20 dorsal 21 lateral 22 frontal 23, 24 ventral 25 retrolateral. Scale bars: 1 mm (20–23); 0.5 mm (24, 25).

Genus *Thyene* Simon, 1885

Diagnosis. Medium-sized spiders, with flattened body. Cephalothorax wide, rounded, abdomen narrower. Leg I hairy, considerably stouter and longer than rest. Characteristic tufts of long black bristles near anterior lateral eyes forming ‘horns’. Structure of genital organs very similar in all members of the genus. Male palp with rounded tegulum twice surrounded by embolus and with single thin tibial apophysis. Species difficult to identify; easier to distinguish by the coloration, especially abdominal pattern, than genital organ structure. The genus includes more than 40 species, the majority distributed in Africa (Wesołowska 2006).

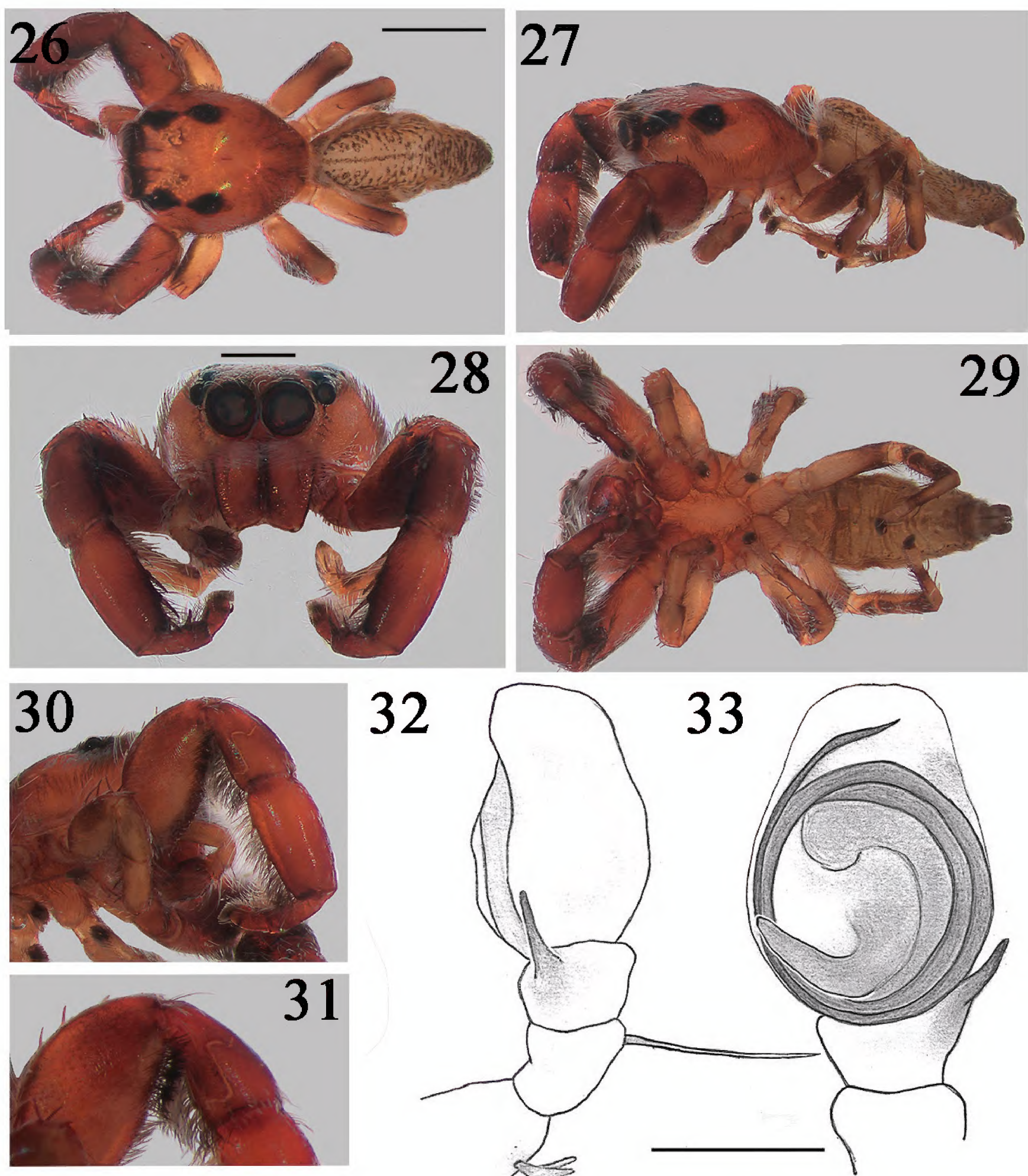
***Thyene volombavatanany* sp. nov.**

<https://zoobank.org/5FE25671-57FC-4440-87F6-B97242C834B2>

Figs 26–31

Material examined. Holotype • ♂ MADAGASCAR; Mahajanga province, Mariarano classified forest; 15.468°S, 46.741°E; 28 June 2017, 20:25; “long grass, net sweep”, Brogan L. Pett leg. (BE_RMCA_ARA.Ara.247708).

Etymology. The specific epithet is a noun in apposition, amalgamating the Malagasy words for “arm” (tanany) and “moustache” (volombava). Reference is made to the extensive hairs on the ventral part of the femur and tibiae.



Figures 26–33. *Thyene volombavatanany* sp. nov. 26–31 male holotype habitus 32, 33 pedipalp 26 frontal 27 lateral 28 dorsal 29 ventral 30- leg I 31 femur I detail 32 retrolateral 33 ventral. Scale bars: 1 mm (26–31); 0.5 mm (32, 33).

Diagnosis. *Thyene volombavatanany* sp. nov. resembles *T. aperta* (G. W. Peckham & E. G. Peckham, 1903) (Ivory Coast, Tanzania, Zimbabwe) by the elongated body, large legs I and in general palpal conformation. Both share a bulb rounded, twice surrounded by embolus running clockwise with narrow, long, flat tegular expansion prolaterally at base. *Thyene volombavatanany* sp. nov. is distinguished by: (i) an abdomen that is generally uniform in colouration with black mottling without white spot (vs. large black area divided into three parts with distinct white spot); (ii) RTA that is approximately the length of the tibia with an apex that is about 1/3 basal tibia width (vs. 1/2 length of tibia and apex under).

Description. Male (holotype). Measurements. CL 2.52, CW 1.94, CH 1.04, SL 1.02, SW 0.48, AL 2.82, AW 1.12. AME 0.44, ALE 0.20, PME 0.09, PLE 0.15. Leg I: 1.22, 0.80, 1.16, 0.76, 0.40. Leg II: 0.88, 0.64, 0.68, 0.42, 0.28. Leg III: 1.04, 0.66, 0.68, 0.76, 0.40. Leg IV: 1.28, 0.64, 0.78, 0.74, 0.40.

Colouration: carapace generally light orangish brown, eyes ringed with dark brown patches, pale streak from fovea to posterior margin; chelicerae orange; sternum, coxae generally pale orange; legs II – IV pale orange-beige with faint brown retro lateral and prolateral patches; labium, maxillae, legs I orangish brown with black ventral femoral setae; abdomen beige with some brown-black mottling; pedipalp orangish-brown. **Carapace:** low and flat, highest at PLE, shallow depression midway between lateral eyes; patches of short thick white setae around fovea, posterior to AME, ventral to PLE, ventral lateral part of carapace; ventral lateral sparse strip of long thin black setae. **Sternum:** broadly oval-shaped, widest between coxae II & III, margin darker orange than centre. **Legs:** Legs I much broader and darker; dense long black ventral setae interspersed with longer sparser white ventral setae on femur, patella, tibia. **Abdomen:** long and thin, more than twice as long as wide; beige with brown-black mottling; long brown lateral setae; brown and white tuft of setae at anterior face. **Pedipalp:** femur slightly longer than patella and tibia together, patella and tibia about the same length; RTA thumb-like, short and rounded; SD arises medially and loops around tegulum for half its length; embolus moderately short and straight, directed prolaterally tapering to a sharp point. **Leg spination:** I: F d3 pl2, P pl1, Ti v4-3, Mt v2-2; II: F d2 pl3, P pl1 (small), Ti pl2 v1-2, Mt v2-2.

New Record

Genus *Plexippus* C. L. Koch, 1846

Plexippus petersi (Karsch, 1878)

Figs 34–36

Euophrys petersii Karsch, 1878: 332, pl. 2, fig. 7.

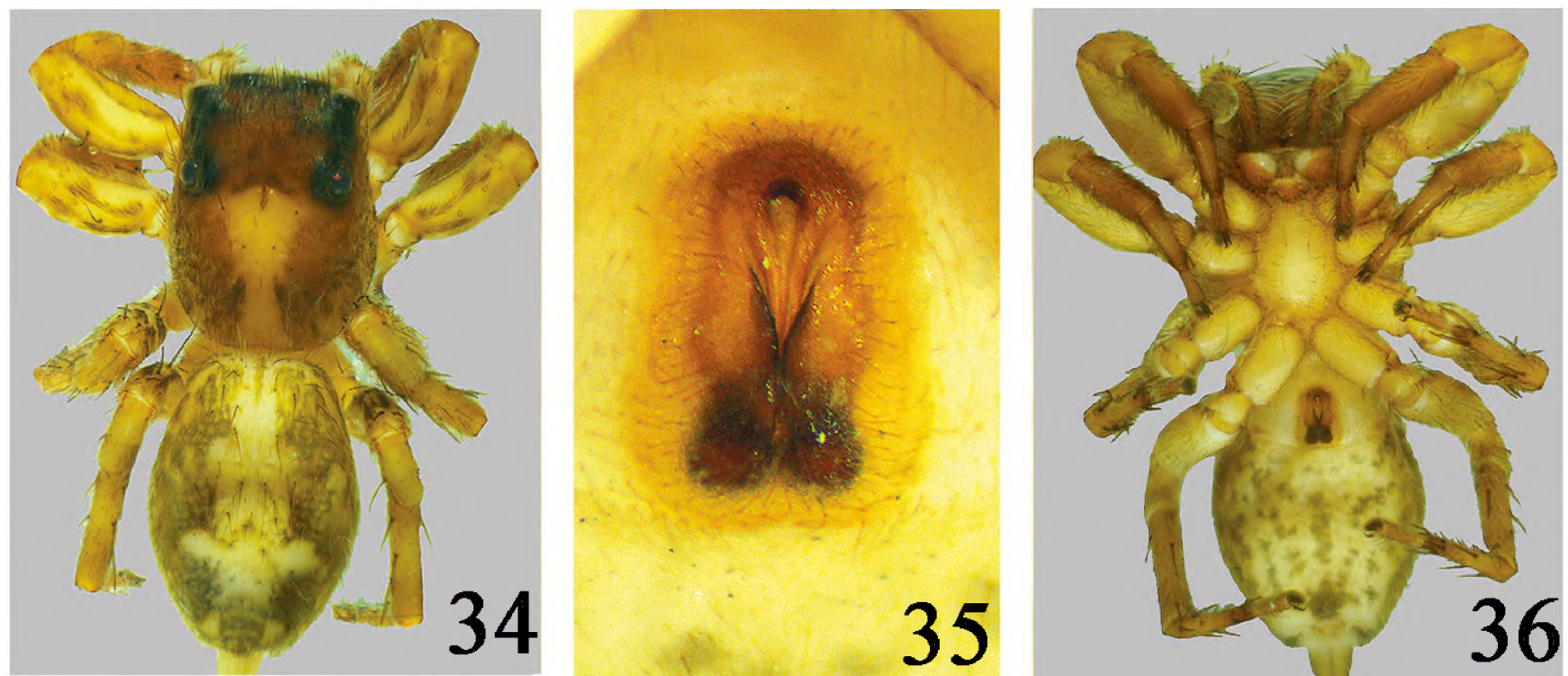
Plexippus petersi Simon 1903: 728.

Marpissa calcutaensis Tikader, 1974: 210, figs 9–10.

Plexippus calcutaensis Nenilin 1984: 6. *Plexippus petersi*: Žabka, 1985: 433, figs 464–470.

Description. See Žabka (1985); illustrated in this paper (figs 34–36).

Material examined. • 1 ♀ Madagascar; Mahajanga province, Mariarano classified forest; 15.470°S, 46.742°E; 21 June 2017, 16:20; Brogan L. Pett leg. (BINCO_MAD_17_0129_1).



Figures 34–36. *Plexippus petersi* (Karsch, 1878) female **34** habitus dorsal **35** epigyne ventral **36** habitus ventral.

Distribution. The species is recorded from many countries across south-eastern Asia (WSC 2024). The only published specimen records in Africa are from Mozambique (Simon 1903), with specimens putatively identified from south-western Kenya, northern Tanzania, and far eastern Madagascar (SMNS database). Thus, this is the first confirmed specimen record from Madagascar.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

KM & BLP primarily identified and diagnosed specimens, KM made the drawings, BLP imaged specimens, both created plates. JET & BLP collected specimens. KM & BLP wrote the first drafts of the manuscript and edited the revised manuscript. JET revised the manuscript and provided in vivo images. All authors conceptualised the study.

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Data availability

All of the data that support the findings of this study are available in the main text.

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